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Does Drought Affect Reproduction in the Saltmarsh Sparrow (Ammodramus Caudacutus)?

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DOES DROUGHT AFFECT REPRODUCTION IN THE SALTMARSH SPARROW (*AMMODRAMUS CAUDACUTUS*)?

by

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ABSTRACT

The Saltmarsh Sparrow (*Ammodramus caudacutus*) is experiencing steep population declines, with extinction likely within the next few decades. Sea-level rise has been identified as a major threat to the species, but little has been done to examine the effects of other aspects of climate change on Saltmarsh Sparrow populations. In this study, I examine whether drought affects reproductive success in the Saltmarsh Sparrow. I use nest- and chick-monitoring data collected over five years across the northern half of the species range to test whether drought conditions affect four metrics of reproductive success in these birds: hatch rate, clutch size, chick growth rate, and fledge. Drought had little to no effect on any metric of reproductive success, though I did detect some minor nonlinear patterns. The results from these analyses suggest that sea-level rise is indeed the largest climate change-related threat faced by this species.

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INTRODUCTION

Global climate change is a major threat to species worldwide, and it has already affected species in many ecosystems. Taxa are experiencing range shifts, changing community assemblages, local extirpations, and extinctions (Parmesan & Yohe 2003, Parmesan 2006, Root *et al.* 2003, Walther *et al*. 2002), and birds are no exception (Crick 2004). Amid warmer temperatures many bird species are laying eggs earlier (Brown *et al.* 1999, Dunn & Winkler 1999), sometimes also causing reductions in chick growth and survival (Gaston *et al.* 2005). Changes in timing of egg-laying, departure from wintering grounds, and migratory route are common and have sometimes resulted in phenological mismatches between life history events and peak food availability (Leech & Crick 2007; Olsen et al. 2015). This (Both *et al*. 2006) and other aspects of climate change, including increasing temperature (Moss *et al.* 2001) and loss of habitat due to shifting vegetation ranges (Lambert *et al.* 2008), have caused population declines in many bird species across multiple ecosystems.

Saltmarshes are one ecosystem strongly affected by climate change and other anthropogenic stressors. Human development of marshland has directly removed large areas of coastal marshes (Gedan & Silliman 2009), and development has brought with it invasive species and pollution, both of which degrade the remaining marsh ecosystem (Gedan *et al*. 2009) and make it more vulnerable to the effects of climate change. A major concern for saltmarshes is sea-level rise. Saltmarshes are divided into two major vegetation zones: a low marsh zone that is flooded twice a day and dominated by seawater-tolerant cordgrass (*Spartina alterniflora*) and a high marsh zone that is flooded

only by the monthly spring tides and dominated by less tolerant species (Bertness & Ellison 1987). As sea levels increase, the marsh becomes more frequently inundated by seawater, and low-marsh cordgrass takes over many high marsh areas (Donnelly & Bertness 2001). In areas bounded on the inland side by human development or steep topography, however, marshes cannot migrate inland and may disappear entirely under the rising sea (Tono & Chmura 2013). Depending on the future trajectory of sea-level rise, salt marshes may be entirely dominated by low-marsh cordgrass or even disappear entirely in some areas in the next century (Donnelly & Bertness 2001). This is a major problem for animals that depend upon the high marsh for any or all of their life cycle.

One such species is the saltmarsh sparrow, *Ammodramus caudacutus*, which nests and forages exclusively in high marsh habitat (Shriver & Hodgman 2010). *A. caudacutus* is a marsh-endemic songbird that inhabits marshes along the eastern coast of North America, with a breeding range from Maine to Virginia, USA (Greenlaw & Rising 1994). Their populations are declining rapidly, at a rate of 9.0% per year, and are predicted to collapse within the next few decades (Correll et al. 2017). Global extinction of the Saltmarsh Sparrow is possible as early as 2035 (Field et al. 2016), and the species is currently under review by the US Fish and Wildlife Service as a candidate for listing under the Endangered Species Act, with a final decision scheduled by the end of 2018 (US Fish and Wildlife Service 2017).

Sea-level rise is identified as the principal threat to the survival of the species (Shriver et al. 2016), and management plans for the species focus on this primary stressor (BirdLife International 2017, Maine Department. of Inland Fisheries and Wildlife 2015, New Hampshire Fish and Game Department 2015), as do conservation management

plans for salt marshes in general (City of New York Parks and Recreation 2017). Though sea-level rise is certainly an important threat, it is important to remember that climate change is a multifaceted issue involving a multitude of other environmental variables that could act as additional stressors upon species, especially those living in an already stressful ecosystem.

Focusing on one stressor alone, like sea-level rise, may lead to inaccurate predictions of species responses, because climate change not only causes variation within individual weather variables but also alters interactions between them (Nadeau & Fuller 2015). In brown trout (*Salmo trutta*) negative effects of high population density on growth are counteracted by positive effects of increased temperatures (Baerum *et al.* 2013), and in forest systems changes in species assemblages can decrease the sensitivity of individual species to abiotic change (Thurm *et al.* 2016).

Harmful changes in multiple variables can also be multiplicative. McCain & Colwell (2011) found that extirpation risk for 16,848 montane vertebrate species was less than 5% due to changes in temperature, but risk was ten times higher on average when changes in a second variable, precipitation, were also taken into account. Changes in combinations of climatic variables (rather than changes in a single variable alone) have been cited as the drivers of range shifts in 464 species of Australian birds (VanDerWal *et al.* 2012). Even when values of temperature and precipitation on their own do not exceed species physiological optima, climatic interactions can prevent species persistence (Smith 2013).

One potential environmental stressor that could alter the impacts of sea-level rise on Saltmarsh Sparrow populations is changing precipitation patterns. Across the United

States, climate change is predicted to significantly alter precipitation regimes (Dore 2005, Trenberth 2011). In the northeast, where Saltmarsh Sparrows breed, total annual precipitation is expected to increase overall, but not evenly across time. Precipitation events are predicted to be more intense and sporadic, with a 70% increase in the amount of precipitation falling during extremely heavy events (defined as the heaviest 1% of all events, Walsh *et al*. 2014). Summers in the northeast are expected to become longer, with higher temperatures and less precipitation (Frumhoff *et al.* 2007). Models predict an increase in consecutive days without precipitation by approximately 10%, indicating that much of the rain that does fall will come in sporadic extreme events rather than being evenly spread across the season (Walsh *et al*. 2014, Horton *et al.* 2014). From an ecological perspective this is problematic, as changes in climatic variability and the frequency of extreme events have been shown to have stronger effects on organisms than simple shifts in mean conditions (Gutschick & BassiriRad 2003, Jentsch *et al.* 2007). At the same time, average annual temperatures are predicted to increase by 1.5º to 5.5º C in the northeast (Horton *et al*. 2014, Walsh *et al*. 2014), which increases the rate at which water is lost from ecosystems by evapotranspiration. In combination, these changes in temperature and precipitation suggest drought may become a concern. Indeed, in the northeastern US, short- and moderate-length droughts are projected to increase in frequency as the planet warms (Hayhoe *et al*. 2007).

It is known that Saltmarsh Sparrow nest success is related to precipitation, with higher probability of failure due to flooding after heavy precipitation events (Bayard & Elphick 2011, Roberts *et al.* 2017). Shriver *et al.* (2016) also observed higher abundances of Saltmarsh Sparrows in years with less precipitation. These studies looked at one

extreme of the precipitation spectrum – heavy rain – but they did not examine drought. Therefore, it is unknown whether the relationship of Saltmarsh Sparrow reproduction with rain is a continuous trend where less rain *always* means higher nest success or if there is a threshold beyond which nest success begins to decline.

There is reason to expect drought to threaten reproductive success, survival, or other parameters of overall species health. Drought has been documented to change avian abundance, species richness, and community composition in ecosystems across the United States (Albright *et al*. 2010). Colón *et al.* (2010) found that the Black-capped Vireo (*Vireo atricapilla*) has lower nest success and fewer nesting attempts in periods of drought. Extended dry periods can also reduce the survival of fledglings and clutch sizes (Vernasco *et al*. 2018). At the population level, drought can drastically change population trends: a study of the Pileated Finch (*Coryphospingus pileatus*) found a more than 50% decrease in survival during a drought year (Tavares-Damasceno 2017). In some cases, drought can better predict avian population decline than temperature (Grinde *et al*. 2017).

Birds do have the ability to deal with the stress of drought to some degree. From a physiological perspective, birds can limit respiratory heat loss in favor of cutaneous heat loss in order to retain some water (Boyles *et al.* 2011). Panting, changing posture, and increasing blood flow to exposed body surfaces are other physiological mechanisms to increase heat loss without losing too much water (Gill 2007). From a behavioral perspective, individuals can seek shade or wet themselves to cool down as well (Dawson 1982), but behavioral thermoregulation is ultimately a tradeoff between retaining moisture while keeping cool and venturing into the heat to obtain food and water. In

extreme cases, this can become a no-win situation, especially when a bird also needs to manage the temperature and water balance of offspring (Cunningham et al. 2015).

Drought paired with high temperature may be an even greater challenge for saltmarsh birds. Most thermoregulation strategies rely on some form of evaporative water loss and/or availability of fresh water (Wolf & Walsberg 1996) and can therefore be exceptionally costly to freshwater-limited species. There is a large body of evidence that saltmarsh birds, Saltmarsh Sparrows included, are strongly freshwater limited and further that the salinity of tidal marshes has played a role in the evolution of their morphology (Greenberg *et al.* 2012a,b, Grenier & Greenberg 2005, Luther & Greenberg 2014, Luther & Danner 2016, Symonds & Tattersall 2010). Saltmarsh Sparrows, however, have no salt glands with which to excrete surplus salt (Goldstein 2006), and they are unable to maintain body weight when forced to consume salt water (Poulson 1969). Saltmarsh Sparrows may thus be particularly susceptible to the stresses of drought, when freshwater limitation would be expected to increase. In the high marsh habitats of this species, drought can create extremely hypersaline conditions between spring tides.

The effects of drought on birds vary across different life stages. Eggs are particularly vulnerable as they are effectively ectothermic, relying entirely on the incubating parent for thermoregulation (Martin et al. 2007). At high temperatures, embryo organs begin to shut down and the blood coagulates (Webb 1987). High ambient temperatures during incubation can increase eggs inviability (DuRant et al. 2010, Hopkins et al. 2011). Eggs can also lose water by evaporation through the shell, especially when the nest has low humidity (Rahn *et al.* 1976). This has been found to induce dehydration in embryos and inviability (Soliman *et al*. 1994, Davis *et al*. 1988).

As a result, it is likely that fewer eggs in a clutch will successfully hatch during periods of drought.

Clutch sizes tend to be smaller in periods of greater heat or lower humidity. This may be a strategy to prevent egg inviability. Incubation often begins with the laying of the penultimate egg (true in Saltmarsh Sparrows, Greenlaw & Rising 1994), which means that earlier laid eggs are exposed to ambient temperatures for longer time. By laying smaller clutches the female can reduce the time the first egg is exposed to harmful ambient temperatures (Cooper et al. 2006). This pattern is seen between coastal and inland populations of swamp sparrows; coastal populations experience higher temperatures and have smaller clutch sizes than their inland counterparts (Olsen et al. 2008). Clutch size is involved in egg water balance as well. The incubating parent's presence creates a moist microclimate in the nest, but the parent's ability to do so is determined by the number of eggs in a clutch, where larger clutches are more poorly regulated (Reid *et al.* 2000). In addition, eggs represent a significant investment of water by the female, with water comprising 80% to 85% of the egg's mass (Carey *et al*. 1980). Therefore, water-stressed females may simply be unable to make a large number of eggs.

Evaporative loss of water from the egg can reduce chick size at hatching (Davis *et al*. 1988, Tullett & Burton 2008). This affects chick growth by changing the starting mass: chicks that developed as embryos under drought conditions are smaller than those that developed under optimal conditions. Also, drought may increase marsh water salinity (Van Dolah et al. 2006), which has been associated with reductions in sparrow nestling growth rate in salt marshes (Olsen 2007). This has been seen in other systems as well. Common Fiscal nestlings (*Lanius collaris*) show reduced growth rates during periods of

heat stress, due to reduced feeding by parents that were heat stressed themselves (Cunningham et al. 2013). High levels of heat and dehydration have been associated with stunted growth in Spotless Starlings (*Sturnus unicolor*) as well (Salaberria *et al*. 2014).

In many birds, drought has been documented as a cause of chick failure. Nestlings do not have the ability to leave the nest to seek water on their own (Martin *et al.* 2007). As a result, younger life stages feel the effects of drought particularly strongly. Downs *et al.* (2015) found that during periods of drought, Cape Parrot (*Poicephalus robustus*) juveniles were more susceptible to disease. Death by evaporative water loss is also possible when temperatures increase or humidity decreases (Bartholomew & Cade 1963). Small desert passerines experience significant evaporative water loss per unit mass, and the problem is exacerbated when birds must leave shady refugia to obtain water (Albright *et al.* 2017). Young birds are particularly susceptible to water loss across the skin, before it develops its water-resistant cornified layer (Dawson 1982). This is true even in wetland ecosystems; Bildstein *et al*. (1990) observed high rates of chick death and abandonment in coastal colonies of White Ibis (*Eudocimus albus*) during periods of drought.

In this study I attempted to quantify effects of drought on Saltmarsh Sparrow reproduction. I compared four measures of reproductive success, which have been reported as sensitive to drought in songbirds, to local conditions at sites from Maine to New Jersey, USA, covering five summers from 2011 to 2015. I hypothesized that drought conditions negatively affect *A. caudacutus* reproduction, where under drought conditions:

1. fewer eggs will hatch,
2. clutches will be smaller,
3. chicks will develop more slowly, and
4. fewer chicks will fledge.

METHODS

Field Data Collection

From 2011 through 2015, researchers searched saltmarshes at 26 sites across the Northeastern United States (Figure 1), for nests of marsh-nesting birds. They visited these nests every three to four days, noting the status of each egg or chick (alive or dead) at each visit and if dead, the cause of death (flooded, depredated, or unknown). For each nest, observers estimated the date laying began, the hatch date, and the fledge date, when applicable. When possible, the female associated with each nest was identified and banded. Upon completion of the nesting cycle, observers assigned an ultimate fate (depredated, flooded, fledged, or unknown, where "fledged" is defined as having at least one chick leave the nest) based on all available information (see Ruskin *et al.* 2017b for detailed methodology). During the years 2014 and 2015 observers also recorded each chick's age, mass, and the length of the tarsus and wing.

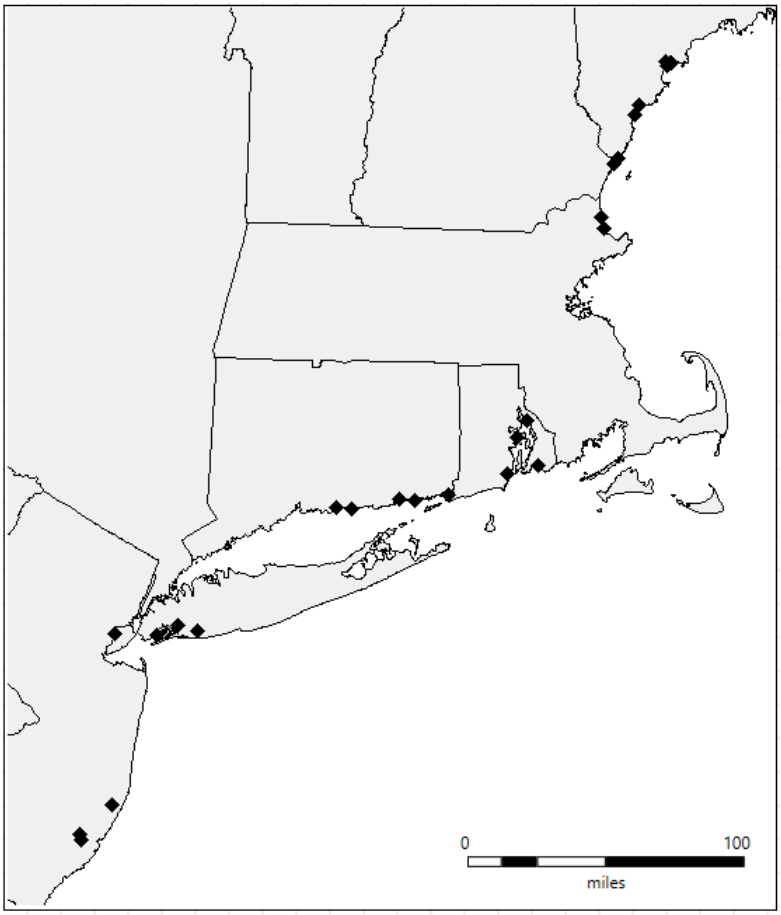

Figure 1. Locations of study sites along the northeast Atlantic coast, USA, from New Jersey to Maine.

In Maine, New Hampshire, and Massachusetts, Saltmarsh Sparrow populations overlap and interbreed with populations of the closely related Nelson's Sparrow (*Ammodramus nelsoni*) (Hodgman *et al*. 2002, Walsh *et al.* 2015). As a result, nests could only be conclusively identified as belonging to a Saltmarsh Sparrow if the female was captured. To determine species of captured females I used a linear discriminant function analysis (LDA) following Walsh *et al*. (2015) to use morphology and plumage characteristics to predict genetic species identity for potentially backcrossed hybrid

individuals. For all analyses, I deal only with nests and individuals identified by this method as Saltmarsh Sparrows.

Drought

The National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (CPC) provides several metrics of drought severity, calculated in slightly different ways. The Palmer Drought Severity Index (PDSI) was created in 1965 by Wayne Palmer, chiefly for agricultural purposes. It takes into consideration several factors affecting soil moisture, including precipitation, temperature, runoff, evapotranspiration, and soil moisture recharge (Palmer 1965). The PDSI cannot be calculated accurately until a wet or dry spell ends and is binary, classifying periods as "drought" or not (Heim 2002). As a result, it is most useful for identifying long-lasting dry spells and gives little information about the severity of drought at a given point during the dry period.

For the purposes of this study I used an adjustment of the PDSI called the Palmer Modified Drought Index (PMDI). The PMDI recalculates the drought index in a continuous manner and is better suited for short timescale, practical purposes that are comparable across regions (Heddinghaus & Sabol 1991). The CPC PMDI values are calculated for each week (Heim 2005) for meteorological regions in each state with similar climates. In this metric, negative values are dry and positive are wet, with values farther from zero in either direction being the most extreme from climatic averages.

Hatch Rate

I defined hatch rate as the number of eggs in a nest to hatch. Because I was interested in eggs that failed to hatch directly due to drought (i.e., were made inviable by

drought rather than were more susceptible to predation or flooding because of drought conditions), I limited this analysis to all nests for which either: 1) at least one egg hatched (indicating the nest had enough time to hatch, and any eggs that did not must be inviable), or 2) all eggs failed for reasons other than depredation or flooding (N = 749). Because drought could act in different ways during different stages of the nest cycle I used three different definitions of drought. I looked at the average PMDI during laying ("Laying Drought") to examine drought's effect on hatch rate while eggs are exposed to ambient conditions, the average PMDI during incubation ("Incubation Drought") to examine drought's effect on nest temperature and humidity during incubation, and the average PMDI from the first egg date to the hatch date ("Egg Drought") to examine the egg period as a whole.

Clutch Size

Saltmarsh Sparrows lay one egg a day (Greenlaw & Rising 1994), and so the number of eggs in a nest can vary between observations during the laying period. Therefore, I defined clutch size as the maximum number of eggs ever observed in a nest to ensure I captured clutch size after laying was complete. I excluded any nests that never had eggs to limit my analyses to nests that were known to be active (rather than built and then abandoned or never used) (N = 1344). Saltmarsh Sparrows are small-income breeders (Greenlaw & Rising 1994), meaning they do not store up energy for the purpose of egg-laying; rather, they are limited in egg production by the resources they have available on the day the nest is initiated. Because clutch size is largely limited by immediately available resources, I defined drought as the PMDI at the nest site on the first day of laying.

Growth Rate

To examine effects of drought on chick growth rate, I looked at all individual chicks that had recorded tarsus length (to the nearest mm), wing chord (to the nearest mm), and body mass (to the nearest 0.1 g) measurements on at least one date (N = 535). I used Principal Components Analysis (function "prcomp" in Program R: R Core Team 2016) to condense these measurements into a single metric of body size that explained 95.8% of the variation in the component variables. I then used a logarithmic transformation (Ricklefs 1967) to convert the growth curve into a straight line for linear modeling. I defined drought as the average PMDI from the hatch date to the date of measurement to isolate the effects of drought during the chick development period.

Fledge Rate

I defined fledge rate as the number of chicks in each nest that survived to fledge. I excluded all nests that failed as eggs, because they had no chicks to fledge or fail. I was specifically interested in the direct effects of drought (i.e., chicks that died directly from exposure to drought conditions, rather than those that were more susceptible to flooding or depredation due to drought). Therefore, I excluded all nests that failed by flooding or depredation from my analyses (N = 408).

I also wanted to see whether drought could indirectly affect fledge rate by changing the probability that a chick will survive a flood event. Saltmarsh Sparrow chicks can climb out of the nest to avoid flood tides as early as day 6 of life (Greenlaw & Rising 1994). If drought slows chick development, six-day-old chicks exposed to drought conditions may not be able to climb out of a nest to escape flooding, while a more developed chick could. I would expect no relationship between success and younger

chicks, because they would be too under developed to climb out of nests regardless of their growth rate. Therefore, I performed a second analysis on nests that failed or fledged when chicks were at least six days old to look for indirect effects of drought on fledge rate. For this analysis, I only included nests that had at least one egg hatch and either failed due to flooding or successfully fledged.

For fledge rate I looked at drought at several life stages, including the three listed above (Laying, Incubation, and Egg). I also tested 1) the effect of the average PMDI from hatch to fledge or fail ("Chick Drought") to examine the influence of drought on growing chicks and 2) the effect of average PMDI from first egg date to fledge or fail ("Life Drought") to examine the cumulative effect of drought experienced across the chick's entire life.

Statistical Analyses

For all metrics of reproduction, I used a linear mixed model (function "lmer" in Program R package "lme4": Bates *et al.* 2015) in Program R (R Core Team 2016) to test whether drought affected reproductive success. I included latitude, year, and first egg date as fixed effects to control for known differences in reproductive success along latitudinal and seasonal gradients (Ruskin *et al*. 2017b), and to control for variation among years. I scaled first egg date and latitude so that their variances (and the effects of those variances) were comparable. I also included female band number and site as random effects to control for differences among sites and parents. Latitude and PMDI are highly correlated (Pearson $r = 0.51$), where PMDI increases (becomes more wet) as latitude increases. To separate the effects of each, I ran models with both latitude and PMDI and with each alone.

For hatch rate, I ran separate models for each drought metric (Laying Drought, Incubation Drought, Egg Drought) and for the combination of Laying and Incubation Drought, to test which life stage was most sensitive to drought conditions, or if the conditions during those life stages interacted. I included clutch size in all models to control for differences among nests (e.g., a nest with a clutch size of two cannot hatch four eggs).

For fledge rate, I ran separate models for each drought metric (Laying Drought, Incubation Drought, Egg Drought, Chick Drought, and Life Drought) and for all logical combinations of those metrics (Laying and Incubation; Laying, Incubation, and Chick; and Egg and Chick) to see which life stage or interactions among life stages best predicted fledge rate. I included number of chicks hatched to control for differences among nests (e.g., a nest with one hatched chick cannot fledge three chicks).

For growth rate, I included chick age as an interaction term with drought to test whether the relationship between chick size and chick age varied under different drought conditions. I also included nest ID as a random effect to control for dependence within broods.

I compared model fit using Akaike's Information Criterion (AIC, Akaike 1973), considering models with a $\Delta AIC \leq 2.0$ to be equivalent. I also created a null model that contained neither PMDI nor latitude to act as a baseline for comparison.

Linear models treat the dependent variable as continuous, even if it is functionally categorical. For example, clutch size is treated as if all numeric values are possible even though only whole integer values can exist in a real nest– a nest can't have 2.37 eggs. To look for nonlinear patterns between the three functionally categorical metrics of

reproductive success (clutch size, chicks hatched, and chicks fledged) and PMDI, I ran *post hoc* models with the dependent and independent variables reversed (predicting drought by clutch size, for example) so that the independent variable was categorical and the dependent variable was continuous. For these models I only included the drought metric that came out as the best predictor of reproductive success in the initial models. I included scaled first egg date and scaled latitude as fixed effects to control for known seasonal and latitudinal gradients of drought.

RESULTS

In total I looked at 1344 active Saltmarsh Sparrow nests from 26 sites in seven states, covering the summers of 2011–2015. Across these states and years the PMDI ranged from -3.47 (severe drought) to 3.18 (very moist).

Hatch Rate

For hatch rate, I analyzed 749 nests across 25 sites in seven states. The top-ranked model was the null, though a model including average drought during the period of laying (but not latitude) was found to be equivalent (Table 1, Figure 2). In the equivalent model, first egg date was negatively (ß ± SE = -0.01 ± 0.05) correlated with hatch rate. Clutch size (ß ± SE = 0.67 ± 0.06) and Laying Drought (ß ± SE = 0.09 ± 0.04) were positively correlated with hatch rate. *Post hoc* tests suggested the possibility of some difference in drought (averaged across the laying period) and hatch rate (Figure 3).

Model	K	ΔAIC	w_i
*Null**	*9*	*0.00*	*0.481*
Avg PMDI (Laying)	*10*	*1.89*	*0.187*
Latitude	10	2.60	0.131
Avg PMDI (Egg Period)	10	3.94	0.067
Avg PMDI (Incubation)	10	4.23	0.058
Avg PMDI (Laying) + Avg PMDI (Incubation)	11	5.80	0.026
Avg PMDI (Laying) + Latitude	11	5.90	0.025
Avg PMDI (Egg Period) + Latitude	11	7.64	0.011
Avg PMDI (Incubation) + Latitude	11	7.86	0.009
Avg PMDI (Incubation) + Avg PMDI (Laying) + Latitude	12	9.39	0.004

* AIC = 2503.75

Table 1. Model rankings for all models of hatch rate. Top-ranked models are italicized. Latitude is scaled. All models also included scaled first egg date, year, and maximum observed clutch size as fixed effects; and study site and identification of the mother as random effects.

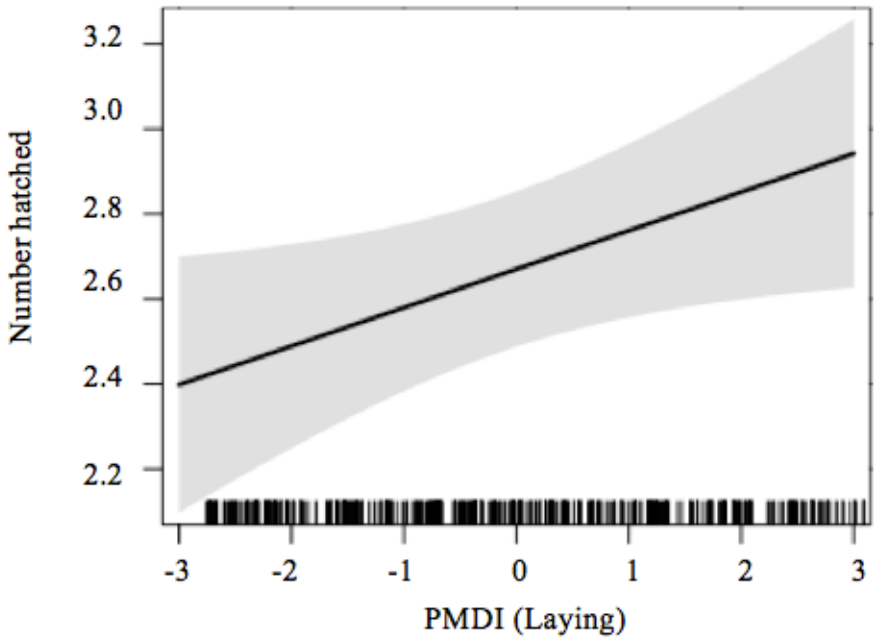

Figure 2. Number of chicks hatched as a function on drought averaged across the laying period, controlling for latitude, first egg date, clutch size, female, and site. Includes best-fit line and 95% confidence interval

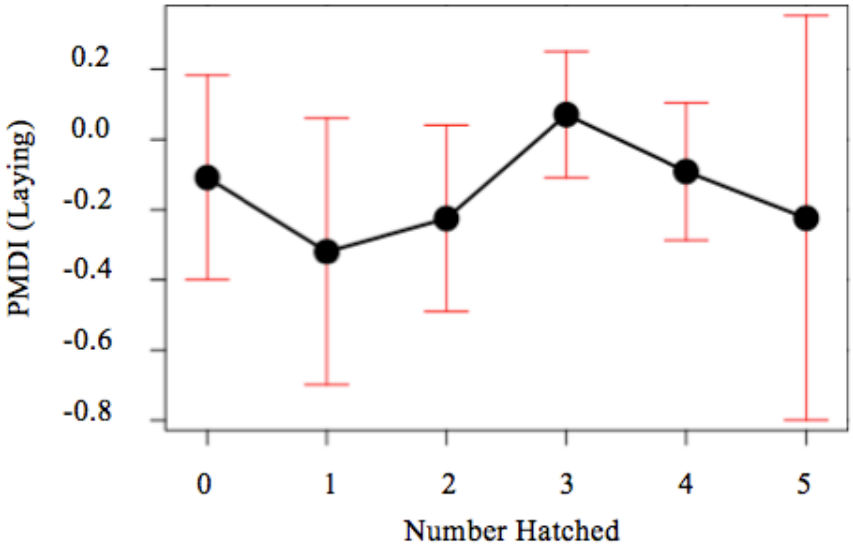

Figure 3. Drought averaged across the period of laying as a function of number of chicks hatched, controlling for first egg date and latitude. Error bars represent 95% confidence intervals.

Clutch Size

The top-ranked model included latitude but not drought (ΔAIC from null model = 10.44, Table 2). Latitude was positively correlated with clutch size (ß ± SE = 0.20 ± 0.04), and first egg date was negatively correlated with clutch size (ß ± SE = -0.29 ± 0.02). The model containing drought but not latitude performed worse than the null (ΔAIC = 6.79, Figure 4). However, *post hoc* tests indicated the possibility of a small nonlinear pattern (Figure 5).

Model	K	ΔAIC	w_i
*Latitude**	*9*	*0.00*	*0.9765*
Latitude + PMDI	10	7.99	0.0180
Null	8	10.44	0.0053
PMDI	9	17.23	0.0002

* AIC = 3299.30

Table 2. Model rankings for all models of clutch size. Top-ranked model is italicized. Latitude is scaled. All models also included scaled first egg date, year, and maximum observed clutch size as fixed effects; and study site and identification of the mother as random effects.

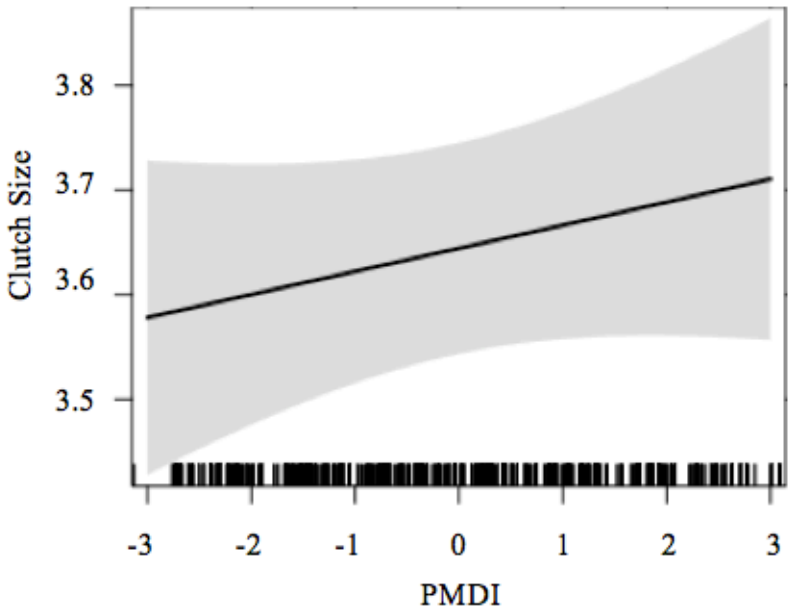

Figure 4. Clutch size as a function on drought on the first day of laying, controlling for latitude, first egg date, female, and site. Includes best-fit line and 95% confidence interval.

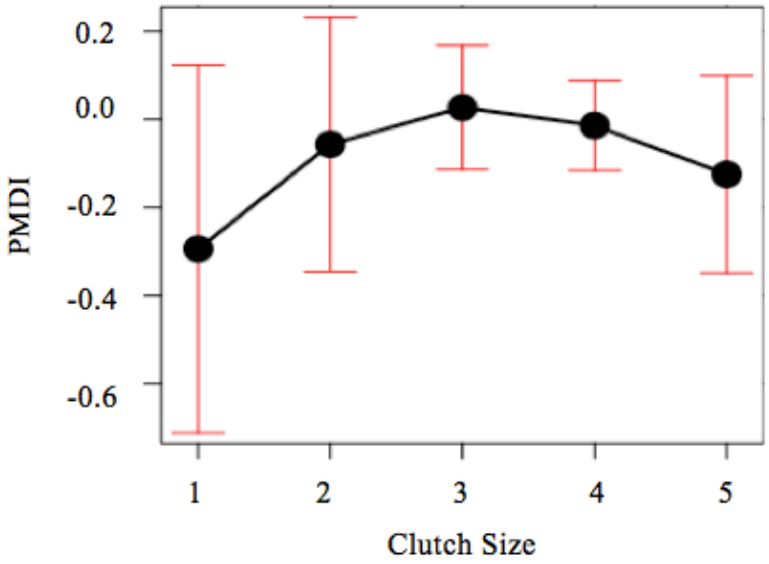

Figure 5. Drought on the first day of laying (PMDI) as a function of clutch size, controlling for first egg date and latitude. Error bars indicate 95% confidence intervals.

Growth Rate

I analyzed 535 chick measurements from 117 nests at 13 sites in five states (New Jersey and Rhode Island were excluded due to lack of data). The best model was the null, including neither drought nor latitude. The model including drought but not latitude performed more poorly than the null (AIC from the null model = 12.8, Table 3).

Model	K	ΔAIC	w_i
*Null**	*7*	*0.00*	*0.9983*
Latitude	8	13.63	0.0011
PMDI	8	14.96	0.0006
Latitude + PMDI	9	27.17	0.0000

*AIC = -1207.922

Table 3. Model rankings for all models of chick growth rate. Top-ranked model is italicized. Latitude is scaled. All models also included chick age, scaled first egg date, and year as fixed effects; and study site, mother, and nest as random effects. Age was included as an interaction term with drought and with latitude.

Fledge Rate

To examine whether drought affects fledge rate, I analyzed 408 nests across 24 sites in 7 states. Here, the best model contained the additive effects of PMDI averaged across the laying, incubation, and chick periods separately, and it did not include latitude (ΔAIC from the null model = 9.05, Table 4). Average drought during incubation was negatively correlated with number fledged (ß ± SE = -0.52 ± 0.17, Figure 7), while first egg date (ß ± SE = 0.09 ± 0.05), number hatched (ß ± SE = 0.91 ± 0.05), average drought during laying (ß ± SE = 0.48 ± 0.11, Figure 6), and average drought during the chick period (ß ± SE = 0.04 ± 0.10, Figure 8) were positively correlated with number fledged. Again, post-hoc tests indicated slight nonlinear trends (Figures 9-11)

Model	K	ΔAIC	w_i
Avg PMDI (Laying) + Avg PMDI (Incubation) + Avg PMDI (Chick)	*12*	*0.00*	*0.8147*
Avg PMDI (Laying) +Avg PMDI (Incubation) + Avg PMDI (Chick) + Latitude	13	3.17	0.1666
Null	9	9.05	0.0088
Latitude	10	12.04	0.0020
Avg PMDI (Chick)	10	12.10	0.0019
Avg PMDI (Laying)	10	12.32	0.0017
Avg PMDI (Laying) + Latitude	11	13.34	0.0010
Avg PMDI (Egg) + Avg PMDI (Chick)	11	13.79	0.0008
Avg PMDI (Life)	10	14.43	0.0006
Avg PMDI (Incubation)	10	14.71	0.0005
Avg PMDI (Egg)	10	15.06	0.0004
Avg PMDI (Chick) + Latitude	11	15.91	0.0003
Avg PMDI (Egg) + Avg PMDI (Chick) + Latitude	12	17.22	0.0001
Avg PMDI (Life) + Latitude	11	17.77	0.0001
Avg PMDI (Incubation) + Latitude	11	17.97	0.0001
Avg PMDI (Egg) + Latitude	11	18.07	0.0001

* AIC = 1133.229

Table 4. Model rankings for all models of fledge rate. Top-ranked model is italicized. Latitude is scaled. All models also included scaled first egg date, year, and number of chicks hatched as fixed effects; and study site and mother as random effects.

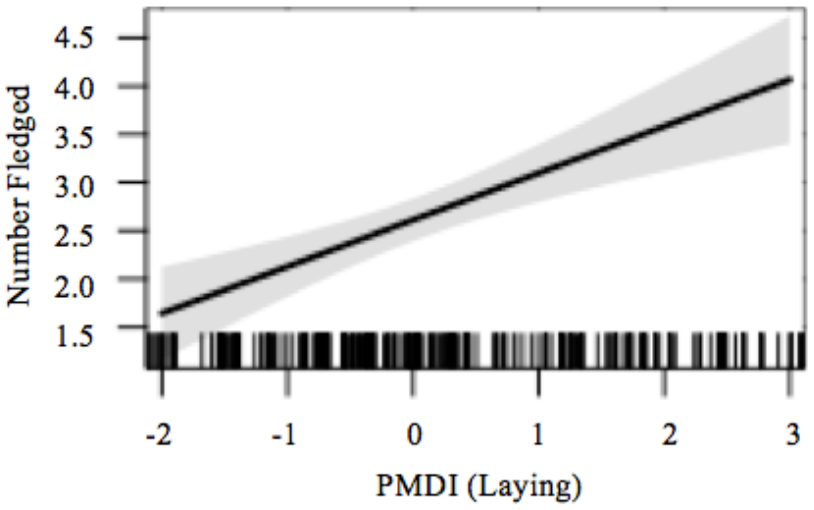

Figure 6. Number of chicks fledged as a function of drought averaged across the laying period, controlling for number of chicks hatched, first egg date, year, study site, and mother.

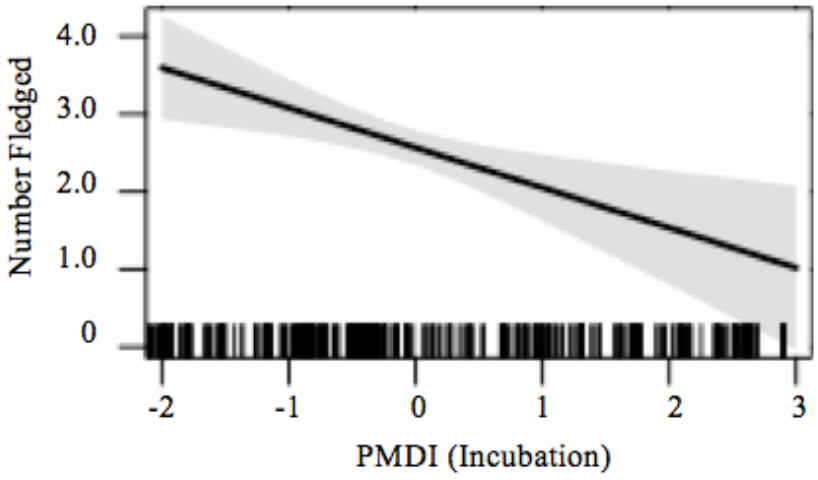

Figure 7. Number of chicks fledged as a function of drought averaged across the incubation period, controlling for number of chicks hatched, first egg date, year, study site, and mother.

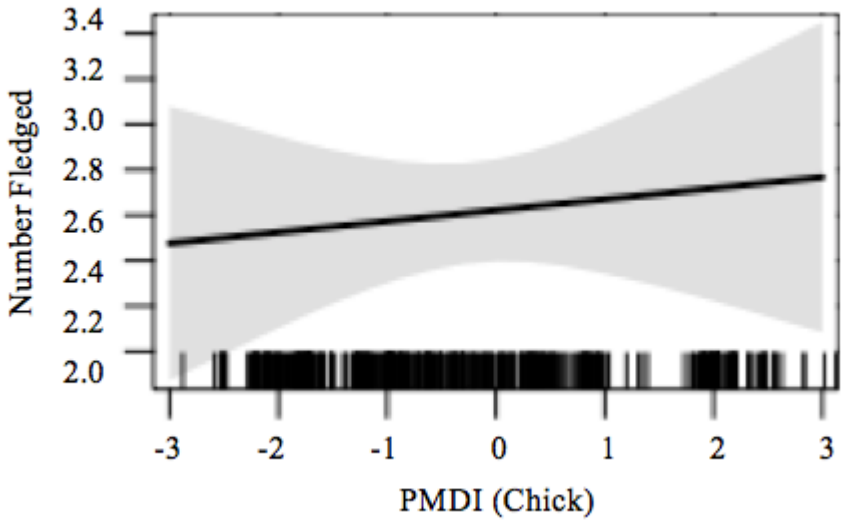

Figure 8. Number of chicks fledged as a function of drought averaged across the chick period, controlling for number of chicks hatched, first egg date, year, study site, and mother.

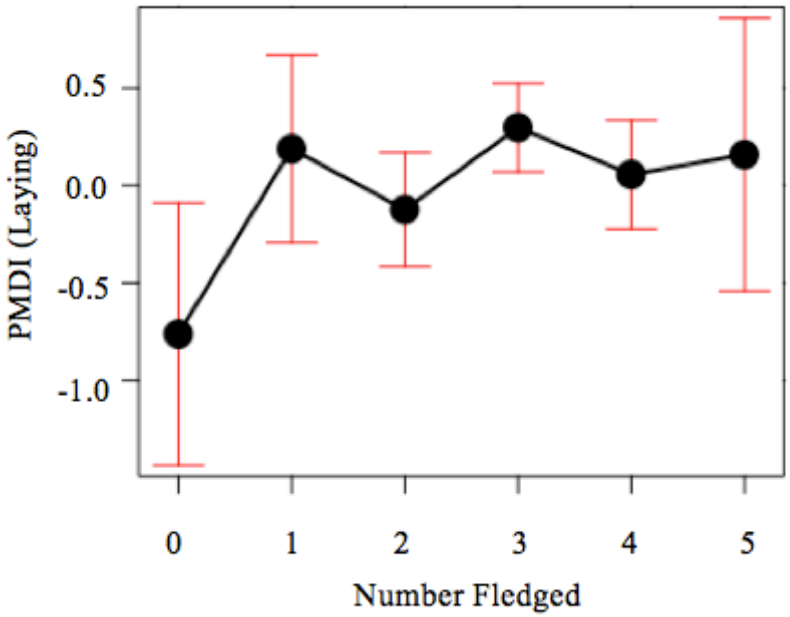

Figure 9. Drought averaged across the period of of laying (PMDI) as a function of number fledged, controlling for first egg date and latitude. Error bars indicate 95% confidence intervals.

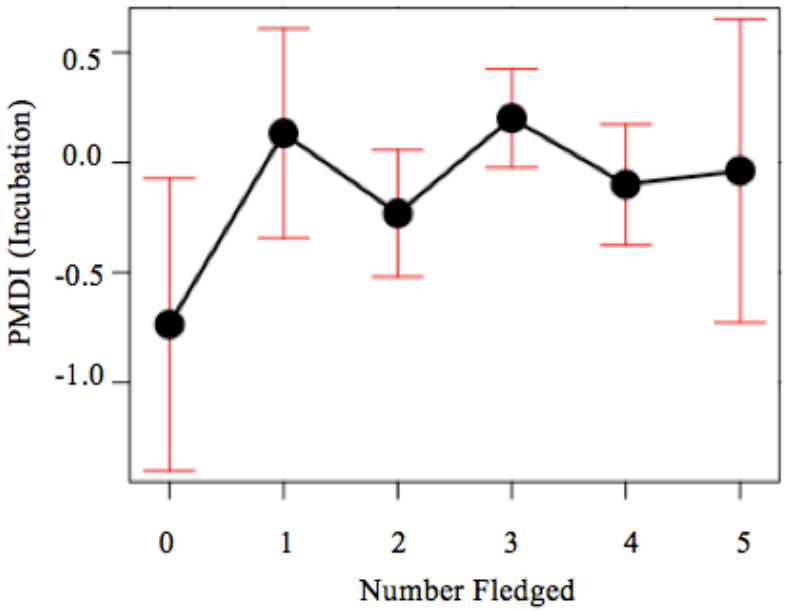

Figure 10. Drought averaged across the period of incubation (PMDI) as a function of number fledged, controlling for first egg date and latitude. Error bars indicate 95% confidence intervals.

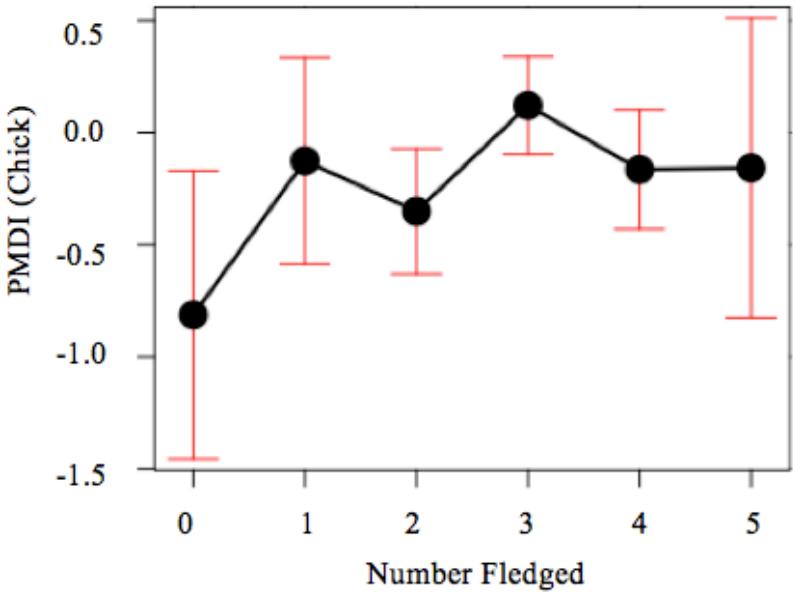

Figure 11. Drought averaged across the nestling period (PMDI) as a function of number fledged, controlling for first egg date and latitude. Error bars indicate 95% confidence intervals.

I performed a second analysis looking only at nests that fledged or flooded when chicks were at least six days old (N = 386), to see if drought affected the probability of flooding. Here the best model contained the PMDI averaged across the laying period, combined with latitude, though the model containing latitude alone was considered equivalent (Table 5). In the model containing drought averaged across the laying period and latitude, latitude (ß ± SE = -0.40 ± 0.10) was negatively correlated with fledge rate; and first egg date (ß ± SE = 0.18 ± 0.06), number hatched (ß ± SE = 0.79 ± 0.06), and PMDI averaged across the laying period (ß ± SE = 0.14 ± 0.05) were positively correlated with fledge rate (Figure 12). Again, *post hoc* tests showed minor nonlinear trends (Figure 13).

Model	K	ΔAIC	w_i
*PMDI (Laying) + Latitude**	*11*	*0.00*	*0.4681*
Latitude	*10*	*1.48*	*0.2234*
PMDI (Egg) + Latitude	11	3.29	0.0903
PMDI (Incubation) + Latitude	11	3.92	0.0660
PMDI (Life) + Latitude	11	4.27	0.0554
Null	9	5.26	0.0338
PMDI (Chick) + Latitude	11	5.95	0.0238
PMDI (Laying) + PMDI (Incubation) + PMDI (Chick)	13	7.51	0.0109
PMDI (Egg) + PMDI (Chick) + Latitude	12	7.64	0.0103
PMDI (Laying)	10	7.98	0.0087
PMDI (Egg)	10	10.43	0.0025
PMDI (Incubation)	10	10.73	0.0022
PMDI (Life)	10	10.82	0.0021
PMDI (Chick)	10	11.24	0.0017
PMDI (Laying) + PMDI (Incubation) + PMDI (Chick) + Latitude	12	13.80	0.0005
PMDI (Egg) + PMDI (Chick)	11	14.31	0.0004

*AIC = 1247.229

Table 5. Model rankings for all secondary models of fledge rate, testing only those nests that fledged or flooded when the chicks were at least 6 days old. Top-ranked models are italicized. All models also included scaled latitude, scaled first egg date, year, and number of chicks hatched as fixed effects; and study site and mother as random effects.

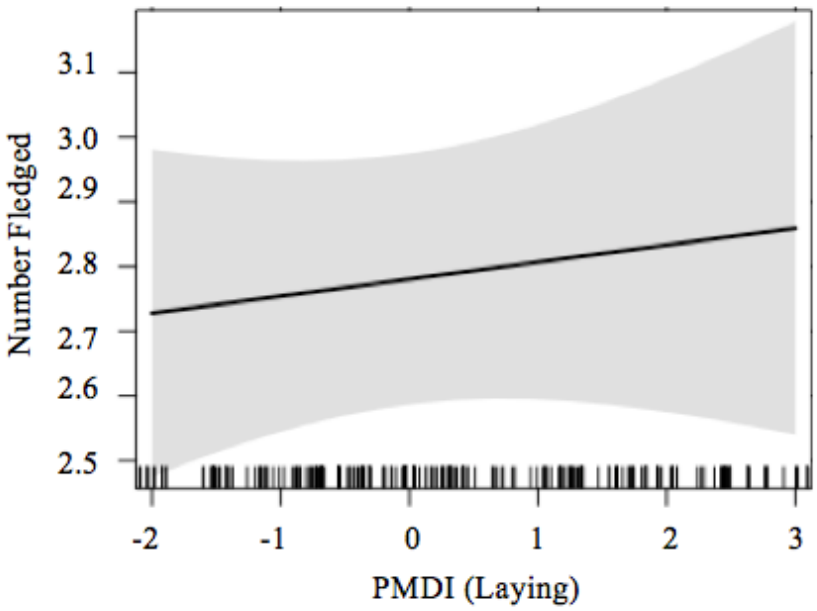

Figure 12. Number of chicks fledged as a function of drought averaged across the laying period, controlling for number of chicks hatched, first egg date, year, study site, and mother. Analysis limited to nests that fledged or flooded when chicks were at least six days old.

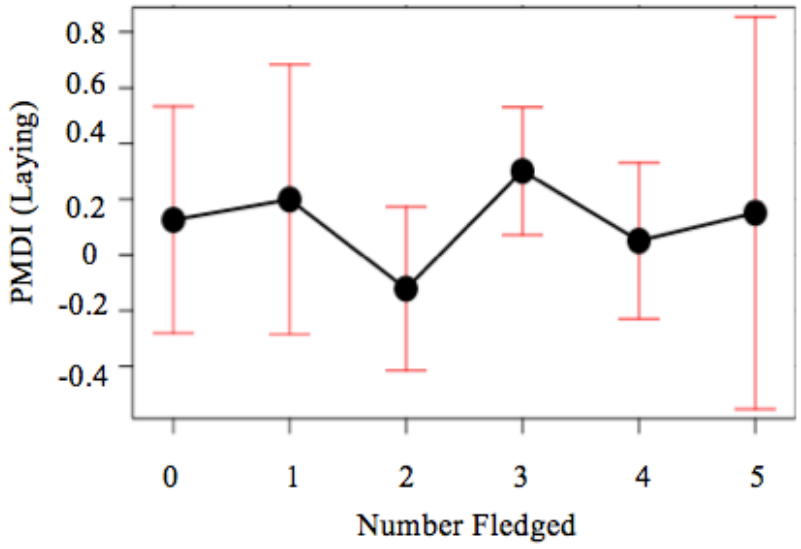

Figure 13. Drought averaged across the laying period (PMDI) as a function of number of chicks fledged, controlling for first egg date and latitude. This analysis considers only nests that failed or flooded when chicks were at least six days old. Error bars indicate 95% confidence intervals.

DISCUSSION

In this study I examined whether drought had an effect on four measurements of reproductive success in the Saltmarsh Sparrow, *Ammodramus caudacutus*. In most initial analyses, drought did not appear to have a significant effect on reproductive output. The only exception to this appeared when analyzing nests that fledged at least one chick or failed for unknown reasons. In this case, the additive effects of average drought during laying, during incubation, and during the chick period predicted fledge rate. However, *post hoc* tests indicated that weak, quadratic patterns may be present, where intermediate clutch sizes, hatch rates, and fledge rates are associated with the highest PMDI values (wettest conditions).

These results suggest two possible situations: either there really is no pattern between drought and reproductive success in Saltmarsh Sparrows, or this study was unable to detect any patterns that do exist. *Post hoc* tests for non-linear patterns did find possible correlations between metrics of reproductive success and drought; clutch size, hatch rate, and fledge rate of 3-egg clutches were all correlated with the highest PMDI values (meaning the wettest periods). It is possible that stronger patterns were not observed because PMDI is calculated so coarsely. In each state, the coastal areas fell into a single drought zone. For example, in New Hampshire the PMDI value used in these analyses was obtained by averaging weather variables across the entire southern half of the state. Precipitation events often occur at a more local scale than this, especially in coastal areas affected by ocean circulation patterns, so these PMDI values may not accurately reflect moisture conditions at study sites. In addition, PMDI is calculated at a

coarse timescale (a week). Because each stage of the Saltmarsh Sparrow nest cycle occurs rapidly (in fact, not much longer than a week), these birds are likely affected by shorter-scale dry spells that are not captured by the weekly PMDI.

On the other hand, it may indeed be the case that reproductive success in the Saltmarsh Sparrow truly is not affected by drought. It is well established that the main causes of nest failure for this species are flooding in the northern half of its range and depredation in the southern half (Ruskin *et al.* 2017a). Any effects of drought may be minor in comparison. I structured my analyses to look for failure due to drought alone. It is also possible that drought makes a nest more susceptible to flooding or depredation. At least one study has found a decrease in marsh elevation during drought periods (Cahoon *et al.* 2011), which could increase flooding risk during the next high lunar tide. Conversely, terrestrial predators like skunks, raccoons, and fox may have greater access to the marsh during the driest times. My analyses were not designed to detect such patterns.

In addition, Saltmarsh Sparrows may be well adapted to surviving on very little water. This species is believed to get much of their water needs from food (Greenlaw & Rising 1994), and short-term droughts may not affect water content of insects or plant material. Seaside and Savannah sparrows, which are also Emberizid sparrows like *A. caudacutus*, can live for extended periods in the lab on very saline water while still maintaining body weight (Cade & Bartholomew 1959, Poulson & Bartholomew 1962). While some tests indicate that Saltmarsh Sparrows do not have this ability over extended periods (Poulson 1969), it is possible that they can tolerate salt water for short periods.

These analyses suggest that drought is not a major threat for the rapidly declining Saltmarsh Sparrow. Still, it is important to remember that this was only a correlative study. Because *post hoc* tests revealed small, nonlinear patterns, further analysis is needed to confirm that drought is not a threat to this species. If at all possible, these analyses should quantify drought at a finer scale, both spatially and temporally. PMDI values calculated daily for each specific site would be ideal. In addition, these analyses only considered the northern half of the Saltmarsh Sparrow's range. Future study should consider the entire range, as drought is more severe in the south.

While this study found no effect of drought on Saltmarsh Sparrow populations, drought is an important ecological force that is predicted to increase as the climate warms. Many saltmarsh species other than the Saltmarsh Sparrow are in decline, and research surrounding their populations principally focuses on sea-level rise alone. It is unknown how drought and other climatic variables might interact with sea-level rise to cause further declines. Further research considering multiple aspects of climate change is essential to successfully monitor and conserve their populations.

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APPENDIX A

PROTOCOL NUMBER: A2011-04-02

Course/Project Title: **Nesting Ecology and Growth Rates of Saltmarsh and Nelson's Sparrows**

PI: **Nesting Ecology and Growth Rates of Saltmarsh and Nelson's Sparrows**

For Committee Use Only:

Date of IACUC Receipt: 3/22/2011 Date of IACUC Review: 4/22/11

Committee Action:

____ 1. Approved until _____
Species and # of animals approved: _____

✓ 2. Modifications required.
Modifications accepted for approval: 5/2/2011 Approved until: 5/1/2014
Species and # of animals approved: Saltmarsh, 1380 adults, 540 chicks

____ 3. Disapproved. See attached statement. Nelson's Sparrows, 1380 adults, 540 chicks

____ 4. Reviewed and determined not to fall under the Policies and Procedures for the Humane Care and Use of Animals (explanation) _____

_____

Full IACUC Review: 4/22/11 Designated Member Review: 5/2/11 by A Elskus

IACUC Signatures:

PROTOCOL.DOC August 2010

ASSURANCES FOR THE HUMANE CARE AND USE OF ANIMALS

As the Principal Investigator on this protocol, I assure that…

1) I have provided an accurate description of the animal care and use protocol to be followed in the proposed project/course.

2) the activities proposed do not unnecessarily duplicate previous experiments.

3) all individuals named in this application who are at risk will be registered in the Occupational Health and Safety Program.

4) all individuals performing animal procedures described in this application are technically competent and have been (or will be) properly trained in the procedures to ensure that no unnecessary pain or distress will be caused as a result of the procedures.

5) I will obtain approval from the IACUC before initiating any changes to this protocol.

6) I am familiar with and will comply with the *University of Maine's Policies and Procedures for the Humane Care and Use of Animals*, and I assume responsibility for compliance by all personnel involved with this protocol.

7) I have read and will follow the appropriate guidelines for the proposed species.

8) if using laboratory animals, all personnel handling the animals have had a tetanus shot within the past ten years.

9) all applicable rules and regulations regarding radiation protection, biosafety, recombinant issues, hazardous chemicals, etc., have been addressed in the preparation of this application and the appropriate reviews have been initiated.

10) animals will be purchased only from licensed, reputable vendors. If animals are purchased form a pet store, the pet store has been informed (in writing) that the animals will be used for research or teaching purposes.

11) I will maintain appropriate animal records (e.g., census, health, veterinary care, euthanasia, surgery, diagnostic, anesthesia, etc.)

12) **I will report at once to the IACUC any unanticipated harm to animals.**

21 Mar 2011

Signature of Principal Investigator/Instructor **Date**

I hereby confirm that I have read this protocol and my signature denotes departmental approval of this project.

3/21/11

Signature of Department Head/School Director **Date**

PROTOCOL NUMBER: A2014-05-07

Course/Project Title: Geographic Variation in Tidal-marsh Sparrow Mating Systems

PI: Olsen, Brian

For Committee Use Only:

Date of IACUC Receipt: 4/23/14

Committee Action:

____ 1. Approved until _____
Species and # of animals approved: _____

✓ 2. Modifications required.
Modifications accepted for approval: 6/23/14 Approved until: 6/22/17
Species and # of animals approved: Sharp-tailed sparrows 900 adults, 1800 nestlings

____ 3. Disapproved. See attached statement.

____ 4. Reviewed and determined not to fall under the Policies and Procedures for the Humane Care and Use of Animals (explanation) _____

Full IACUC Review: 5/29/14 Date

Designated Member Review: 6/23/14 date

Member: M. Kinnison

IACUC Signatures:

August 2013

ASSURANCES FOR THE HUMANE CARE AND USE OF ANIMALS

As the Principal Investigator on this protocol, I assure that…

1) I have provided an accurate description of the animal care and use protocol to be followed in the proposed project/course.

2) the activities proposed do not unnecessarily duplicate previous experiments.

3) all individuals named in this application who are at risk will be registered in the Occupational Health and Safety Program.

4) all individuals performing animal procedures described in this application are technically competent and have been (or will be) properly trained in the procedures to ensure that no unnecessary pain or distress will be caused as a result of the procedures.

5) I will obtain approval from the IACUC before initiating any changes to this protocol.

6) I am familiar with and will comply with the *University of Maine's Policies and Procedures for the Humane Care and Use of Animals*, and I assume responsibility for compliance by all personnel involved with this protocol.

7) I have read and will follow the appropriate guidelines for the proposed species.

8) if using laboratory animals, all personnel handling the animals have had a tetanus shot within the past ten years.

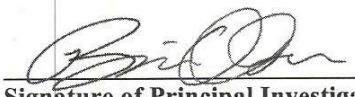
9) all applicable rules and regulations regarding radiation protection, biosafety, recombinant issues, hazardous chemicals, etc., have been addressed in the preparation of this application and the appropriate reviews have been initiated.

10) animals will be purchased only from licensed, reputable vendors. If animals are purchased form a pet store, the pet store has been informed (in writing) that the animals will be used for research or teaching purposes.

11) I will maintain appropriate animal records (e.g., census, health, veterinary care, euthanasia, surgery, diagnostic, anesthesia, etc.)

12) **I will report at once to the IACUC any unanticipated harm to animals.**

13) I acknowledge that in the event of a disaster (natural or man-made) it may become necessary to triage, euthanize or otherwise modify the care and disposition of the study animals in order to avoid unacceptable pain or distress. I delegate overriding authority for emergency decisions of animal disposition to the Institutional Veterinarian or his/her designated representative.



21 April 2014

Signature of Principal Investigator/Instructor **Date**

I have read this protocol and my signature denotes departmental approval of this project.

21 April 2014

Signature of Department Chair/School Director* **Date**

***If PI is Chair/Director, form must be signed by Dean.**

AUTHOR'S BIOGRAPHY

Val "Bivalve" Watson was born to American parents in a stopped train car on the border of Egypt and Switzerland and thus obtained triple citizenship, which she gave up at the age of six to become a Citizen of the World. She graduated from Norfolk County Agricultural High School in 2014 with a major in Plant Sciences and a concentration in aggravating administrators. Between high school and college, Bivalve took a gap year to raise yaks in the Himalayas, but finding them rather disagreeable came back to the states after a year to continue her schooling. At the University of Maine, Bivalve has a major in Ecology and Environmental Sciences with a dual concentration in general ecosystem ecology and interpretive ecological tap dance. She has been an active member of the UMaine Watermelon Club for four years, serving first as secretary and later taking the lead as Grand Poobah Melonballer. She also founded the Astrophysical Birders club at UMaine and was the brains behind the nefarious Wet Socks Initiative.

During college, Bivalve spent her summers harassing innocent animals in the name of science for projects concerning bumblebee foraging dynamics in high alpine meadows, saltmarsh bird communities, stream invertebrate communities, and coastal Maine intertidal incompetence. After graduation, she plans to spend a few years modeling her life after 16th century dancing cleric Thoinot Arbeau before returning to school to make more of a nuisance of herself.